OBSERVATIONS ON THE PREDATORY BEHAVIOR OF THE SPIDER *HYPOCHILUS GERTSCHI* HOFFMAN (HYPOCHILIDAE)

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The primitive, relict spider family Hypochilidae[2] occurs in the United States (four species), Chile, Tasmania and China (one species each), and exhibits anatomical characters intermediate between the suborders Orthognatha and Labidognatha. Despite the obvious importance of these spiders in evolutionary studies, little has been done to clarify their behavior. Comstock (1940) briefly described the web of *Hypochilus thorelli*. Gertsch (1958) reviewed the taxonomy of the entire family, noting that while all North American members of the family make similar webs (described in detail below), *Hickmania troglodytes* (Tasmania) weaves a large sheet, up to four feet long and two feet wide, and *Thaida peculiaris* (Chile) suspends a large mesh funnel up to three feet in diameter among vegetation (Zapfe & Gertsch, 1955). The web of *Ectatosticta davidi* (China) is unknown. Hoffman (1963) described *H. gertschi* from the Appalachians and noted few differences between its web and that of *H. thorelli*. In 1964, Gertsch described *Hypochilus bonneti* from Colorado, and included excellent photographs of the upper part of the web and of the egg sacs. Kraus (1965) reported briefly on the behavior of captive West Virginia specimens of *H. gertschi* which he had transported to Germany.

This study was carried out approximately two miles north of Athens, Mercer County, West Virginia, in a typical *H. gertschi*

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[2]Marples (1968) recently reclassified this family: *Hypochilus* and *Ectatosticta* are left in the Hypochilidae, and *Hickmania* and *Austrochilus* are placed in their own families, Hickmaniidae and Austrochilidae, respectively. Lehtinen (1967) put each genus in its own family: Hypochilidae, Ectatostictidae, Hickmanidae (sic) and Thaididae (this last is the proper name for the family including *Thaida*, a senior synonym of *Austrochilus*). Marples' study is convincing, that of Lehtinen somewhat superficial. However, neither of these changes affects the family name of *Hypochilus*.

habitat. I have to thank Dr. and Mrs. Jeremiah Blatt for permission to use the site, and Dr. and Mrs. Carl Chapman for their hospitality. Mr. David Bard helped with the photography.

Structure of the web

Hypochilus gertschi is usually found under overhanging rock ledges. While fairly moist localities, such as stream banks, cliffs with seepage flow, etc., usually harbor a few specimens, *H. gertschi* seems to be more common in drier, sunnier locations than *H. thorelli* farther south. Hoffman (1963) commented on this, and I have observed individuals on very dry, south-facing cliffs. On two occasions, I have seen populations fully exposed to sunlight much of the day.

The web of *H. gertschi* is usually described and pictured (Hoffman, 1963; Kraus, 1965) as a "lampshade-shaped" mesh, broadly flared beneath, and attached by its smaller end to the under surface of a rock ledge. At the upper (or inner) attached end of the lampshade, a fine sheet of silk is spun over the substrate. Of all previous published references to the web, only Kraus (1965) mentioned the extensive tangle of threads extending, when the web is under a ledge, to the ground beneath, or to nearby plants.

The webs of *H. gertschi* I observed incorporated these previously described features. The size of the web is proportional to the size of the individual. Webs of large (probably penultimate instar) specimens were about 8 cm in diameter at the open end of the lampshade, and usually about 1 cm less in diameter at the closed end. The main portion of the shade consists of a close, irregular mesh (Fig. 1). The flared end of the lampshade (*A*, Fig. 2) is held taut by 10-15 double support lines (*B*, Fig. 2), attached in pairs to a roughly polygonal frame line (*C*, Fig. 2). The frame line is in turn guyed to the surrounding rock surface and to the extensive tangle below. The tangle (*D*, Fig. 2) is always cone-shaped, with the apex attached below, and the base at the frame line, when the web is placed under a ledge, or so that the plane of the lampshade walls is nearly vertical. When the webs are attached to an almost vertical surface, and the plane of the lampshade walls is nearly horizontal, the spider faces a number of problems in guying the frame line in such a way that the lampshade is held tautly flared. If a reasonably narrow crevice is used, the web can be attached to the opposite wall (Fig. 3). In cases where no such directly opposing surface is available, guy lines are run from the frame line nearly parallel to the surface to which the lampshade is attached until a protrusion in the rock, the surface of a gently sloping rock face, or some other support is reached (Fig. 4). This

Fig. 1. Lampshade portion of *Hypochilus gertschi* web seen from below, powdered with cornstarch. The spider is just above the center of the web; note the effective cryptic coloration. About 2/3 actual size.

may result in lines of extraordinary length, up to 2 m. The opposing lines from the upper side of the frame into the tangle often form a sheet in front of the lampshade part of the web. The spider occupies the center of the lampshade in a typical posture (Fig. 5) and holds the sides of the lampshade near the base with its first 2 pairs of legs. Leg pairs III and IV hold the silk sheeting spun against the substrate.

The distribution of dry and sticky silk in the web was determined by powdering the web with fine cornstarch (Fig. 1). Sticky silk is limited to the shade and its support lines, that is, while the frame line is not sticky, all the lines enclosed by it are. The sticky silk of *H. thorelli* has been described by Comstock (1940) as a hackled band consisting of a warp of four threads, the two outer ones much curled, and a broad woof with undulating edges, composed of sticky silk. This type of thread was found in a sample from the web of *H. gertschi* which also included single smooth lines on which an irregular band of sticky silk had been laid.

Comstock (1940) observed some stages of web construction in the laboratory. He found that the first part of the web was the filmy disc of silk against the substrate. This was followed by construction of the lampshade. I attempted to investigate web construction by destroying established webs and observing the manner in which the spider replaced them. Webs destroyed in late afternoon were replaced the following morning, while those destroyed in the morning were not replaced for about 24 hours. When the web was removed, the spider ran a short distance away on the rock surface. In all of the 11 cases observed, the spider returned to the old web site to build a new web. Unfortunately, web construction takes place at night, and any light on the spiders halts their activities.

Predatory behavior

Remains from undisturbed webs indicate that the main items of prey are small Diptera of various families, Tipulidae, and phalangids of the genus *Leiobunum* (primarily smaller, immature individuals). In addition to these animals, abundant at the study site, experimental prey were obtained by sweeping in an adjacent field. Most of the prey obtained by this method consisted of immature Hemiptera, Orthoptera, and small beetles.

The spiders were first tested for response to prey in the non-sticky tangle below the lampshade. In all cases, the response was the same as to that of a mild threat (see below). At no time did any of the individuals studied leave the lampshade to investigate potential prey

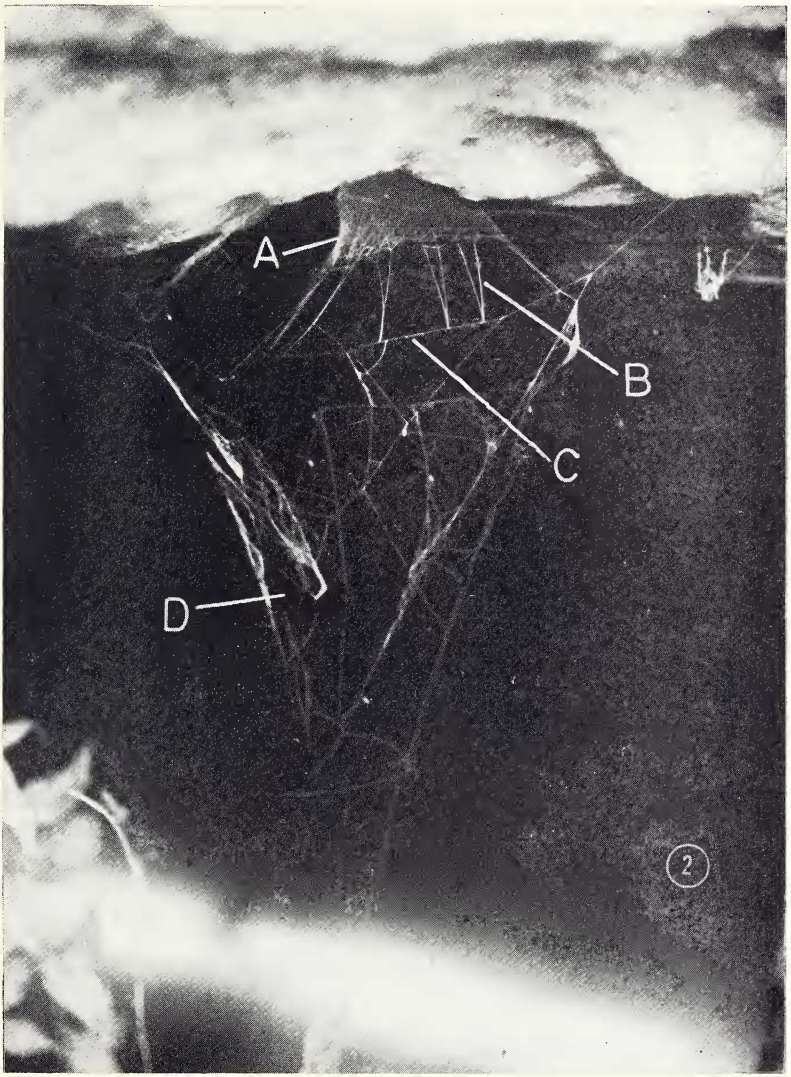
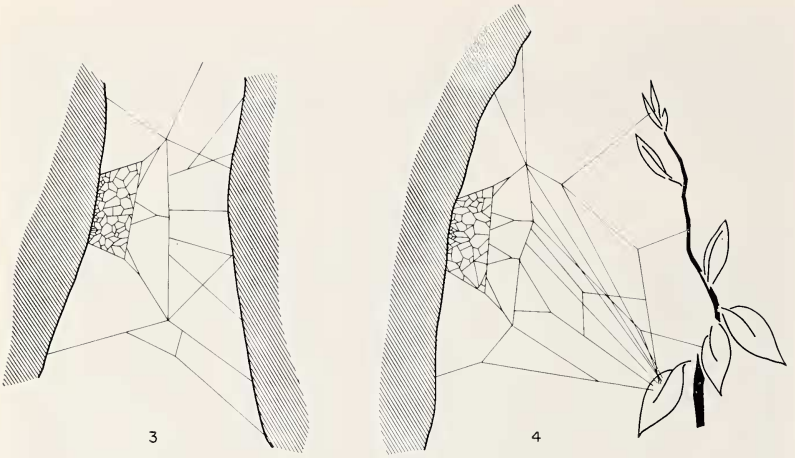


Fig. 2. Entire web of *Hypochilus gertschi* seen from the side. *A*, lampshade; *B*, support lines; *C*, frame line; *D*, tangle. Dimensions about .30 by 1 m.

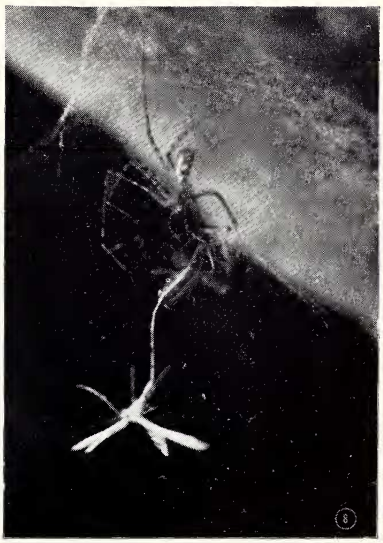


Figs. 3, 4. Webs of *Hypochilus gertschi*. Fig. 3. Web in crevice. Fig. 4. Web on nearly vertical rock face. Drawn from photos.

in the tangle, and as the silk used there is not sticky, most prey animals found it easy to escape, remaining in the tangle a maximum of 80 seconds.

The spider responded to prey only if the prey came in direct contact with the sticky silk of the lampshade. Unless the initial contact was violent, there was no visible response on the part of the spider. The continued struggles of the prey caused a "testing" of web tension by the spider, slowly flexing and extending its legs, and moving the body up and down. Presumably this allowed the spider to sense on which side of the lampshade the prey had been caught. During these motions the spider slowly turned to face the prey (Fig. 6). Up to this point any decrease in prey activity caused the spider to stop what it was doing, to resume its movements only when prey struggles began again.

Once the prey had been touched with the tarsi of the first and second legs, the actions of the spider were more or less continuous. Legs 3 and 4 grasped the opposite side of the lampshade near the base, while legs 1 and 2 pulled on the lampshade threads near the prey. From this position, the spider pulled in the side of the lampshade (Fig. 6) with a very slow, but continuous, movement. When the struggling prey came within reach of the jaws, it was palpated and bitten repeatedly. The use of silk to subdue prey was not observed. Apparently the prey was killed by a combination of biting and poison-



Figs. 5-8. Attack behavior of *Hypochilus gertschi*. Fig. 5. Position of *H. gertschi* in web. Arrow points out that first and second legs hold sides of lampshade. Fig. 6. *H. gertschi* pulling prey to lampshade center. Fig. 7. *H. gertschi* biting prey. Fig. 8. Response to a second prey; see text.

ing (Fig. 7), depending on its size. Three to five minutes after the first bites, the prey ceased its struggles.

If a second prey animal was offered to a spider feeding on one previously caught, it was usually ignored (Fig. 8), except when the spider was almost finished feeding. The spider then attacked, either holding the partially eaten remains, or allowing them to drop. If the second prey was vigorous, and as large or larger than the spider's abdomen, the first prey was merely released and held by the still-attached threads of the lampshade, while a typical attack on a second prey followed. Spiders were not seen to return to the original prey.

Feeding took up to two hours, during which time the prey was reduced to a shapeless mass. After the meal, the spiders drop the ball of remains, and many of these bits of detritus catch in the tangle below.

In some cases, when prey was brought in contact with the palpi and jaws, the spider cut the threads surrounding the prey with its fangs, and dropped the live animal out of the web. This could not be correlated with the species of prey organism or with the feeding state of the spider. The same individual prey animals were captured and fed upon by other *H. gertschi*, and such rejection behavior was observed in spiders that had not fed in at least four hours, as well as those that had just devoured prey. Twice, very active prey was ignored by spiders that had not fed during that day's study period.

The steps in *H. gertschi* predatory behavior consists of a simple sequence summarized in Figs. 9 and 10.

Escape behavior

Since the spiders responded to large, active prey in the tangle as to a mild threat, escape behavior of seven individuals was studied. A "mild threat" consisted of irregular tapping of the frame line and its supports. The primary response, as observed by Kraus (1965), was a vigorous shaking or oscillation of the body and web, as is often seen in *Pholcus phalangioides* (Pholcidae). If the threat continued, the spider moved to the side of the lampshade farthest from the intrusion, facing to the outside. Finally, five of the seven individuals used their chelicerae to cut a hole in the side of the lampshade, through which they escaped to crawl 10 cm to 1 m away from the web site. All seven returned within 20 minutes to the original web.

A "heavy threat" consisted of direct attempt to capture the individual. Upon being touched, the immediate response of the spider was to drop from the web. Usually this resulted in the spider being caught in the lower tangle, where it clumsily struggled until it could

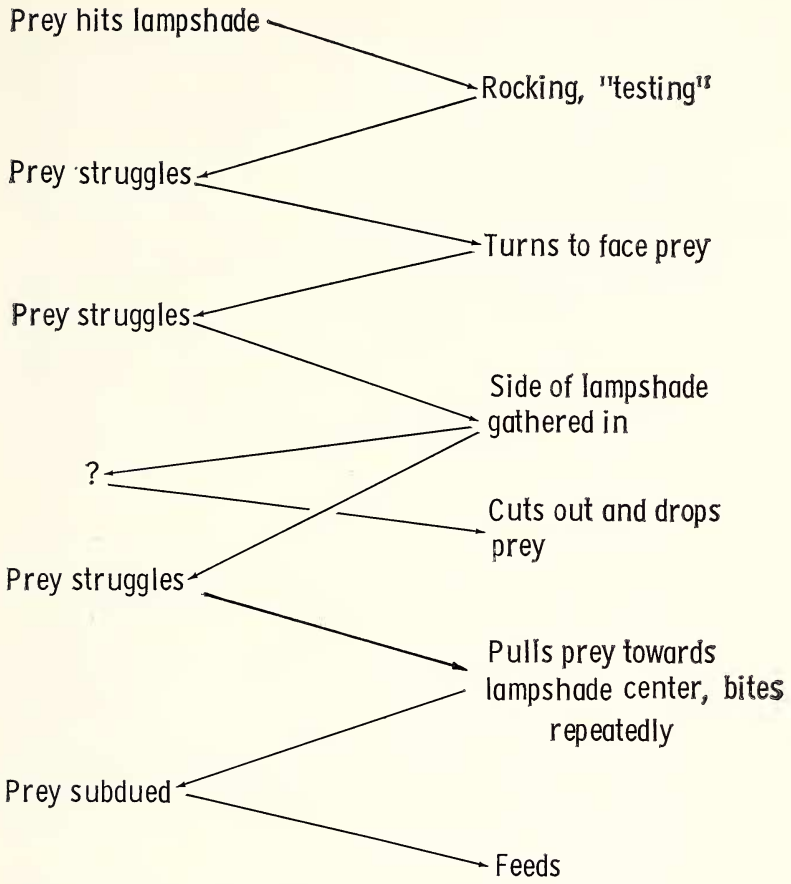


Fig. 9. Typical attack sequence of *Hypochilus gertschi*.

drop to the ground. Once on the ground, the spider remained inert with the legs drawn up over the carapace. Return to the web involved a laborious search for the attachment point of the tangle, which was then climbed until the spider could re-enter the lampshade. In two cases, escaped individuals found the webs of other individuals and attempted to climb them. When they reached the lampshade, they were repulsed by the occupant.

Discussion

According to Marples (1968), the anatomy of *Hypochilus* is the most primitive of any araneomorph spider. The web of *Hypochilus*

might be considered more primitive, despite its apparent complexity, than the webs reported for other Hypochilidae. Following the scheme of Kaston (1964) the web of *Hypochilus* can easily be derived from a few capture lines extending from a silk-lined retreat. Possibly such capture lines, like those found in *Ariadna* (Segestriidae) webs, are homologous to the radial support lines of the lampshade of *Hypochilus*. The lampshade itself may represent an extension of an original silk-lined retreat. The primary function of the extensive lower tangle seems to be support of the lampshade. The more aerial webs of *Hickmania* and *Thaida* are clearly derivative and point up the long history and relict nature of the hypochilids. One is tempted to speculate that hypochilomorph orbweavers may await discovery in some remote area!

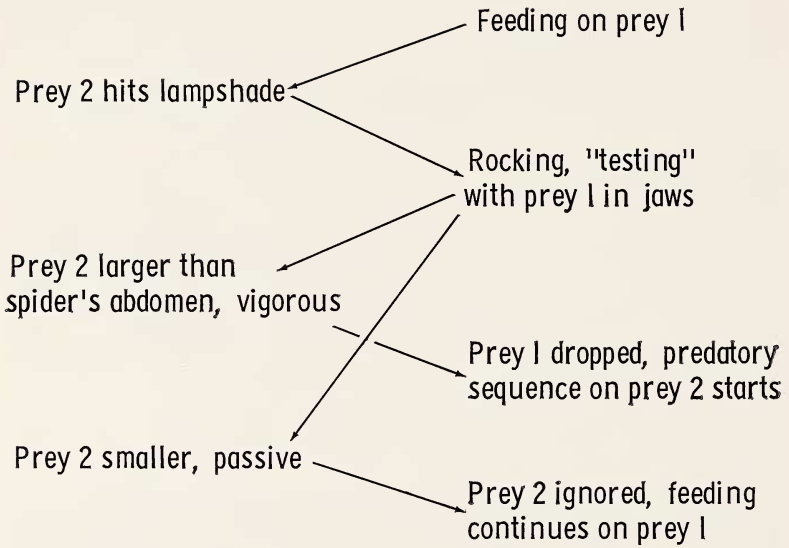


Fig. 10. Response of *H. gertschi* to a second prey.

Eberhard (1967) discussed the evolution of the use of silk as an offensive weapon, relying primarily on observations on *Diguetia*, a primitive, six-eyed, ecribellate spider. He postulated a series of steps through which spiders have come to use silk to subdue prey:

1. No web is spun, prey subdued by biting.
2. Ground webs spun, prey subdued by biting.
3. Aerial webs spun, prey subdued by biting, wrapped to prevent loss during subsequent attacks.

4. Aerial webs built, prey subdued by biting and wrapping.
5. Same as 4, but prey overcome by wrapping only.

Of particular significance is the fact that *Hypochilus*, which builds the most primitive web of those known in its primitive family, has never been observed to use silk as an offensive weapon. Instead, the extreme stickiness of the cribellate silk of the lampshade is relied on to hold prey until it can be bitten to death. *Hypochilus'* response to a second prey, before it has finished feeding on the first, clearly places it between steps two and three in Eberhard's scheme. *Hypochilus* makes an aerial web but either ignores a second prey, or abandons the first to attack the second, the sequences probably dependent on the size and activity of the second prey, and the degree to which the spider has fed on the first. In any case, behavior similar to that seen by Eberhard (1967) in *Diguetia*, in which the original prey is secured to the web by silk to prevent its loss while a second prey is attacked, does not seem to occur in *H. gertschi*.

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